

SPATIAL AND SEASONAL DISTRIBUTION OF PLANKTONIC CLADOCERA IN A SMALL RESERVOIR¹

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ABSTRACT

A planktonic cladoceran community composed of 4 species (*Bosmina longirostris*, *Daphnia parvula*, *Diaphanosoma leuchtenbergianum*, and *Ceriodaphnia quadrangula*) was studied over a 3-year period in a small man-made lake in southwestern Ohio. Plankton samples were collected from 3 stations and 4 depths (surface, 3-, 6-, and 9-meters). *B. longirostris* was the numerically dominant species at all stations and in all seasons, except for a short period in the spring, when *D. parvula* was dominant. *D. parvula* was a vernal species, persisting only in small numbers during the summer and autumn. *D. leuchtenbergianum* was classed as a polythermic species, being present in significant numbers, only during the warmest periods. *C. quadrangula* appeared as a significant member of the community only during the final year of the study.

Diaphanosoma leuchtenbergianum was consistently most abundant at the shallowest of the 3 stations; the other 3 species did not exhibit any consistent pattern of horizontal distribution. *B. longirostris* was very erratic in its vertical distribution from sampling period to sampling period, exhibiting population maxima at 3 of the 4 sampling depths with considerable frequency. Attempts to relate changes in its vertical distribution to environmental conditions were not successful. *D. parvula* populations concentrated with considerable regularity at the 6-meter depth. This was especially true during the 1962 season, in contrast to 1961 and 1963. Data are presented which suggest that, during 1961 and 1963, the species was more frequently prevented from localizing at its preferred depth by vertical turbulence in the water column. Both *D. leuchtenbergianum* and *C. quadrangula* were mid-water forms, population maxima most frequently occurring at 3- and 6-meter depths.

INTRODUCTION

Although there have been many publications devoted to the subject of planktonic Cladocera, most papers fall into one of two broad categories: (1) they are survey studies involving a few samples from a number of bodies of water over a short time interval (e.g. Armitage, 1961) or (2) they are detailed studies of certain facets of the ecology of a single species (e.g. Hall, 1964). The first category is useful in delimiting the geographic range and, sometimes the seasonal distribution and habitat preferences of the various species; the second category has contributed much to our understanding of the ecology of a few species, primarily of the genus *Daphnia*. A few papers have dealt with the topic at the community level and these have been reviewed in an excellent paper by Pennak (1957). There is still, however, a dearth of published information on the ecology of many of the most common species of planktonic Cladocera.

The present paper is based on a three-year study of the planktonic Cladocera of a small artificial reservoir in southwestern Ohio. Only four species of Cladocera have been identified in the planktonic community of this lake, based on an examination of 514 individual plankton samples collected over the three-year period. Relatively little has been published on the ecology of these particular species. Therefore, it is hoped that this description of the temporal and spatial characteristics of this cladoceran community will be useful to others.

This study was carried out in Acton Lake (fig. 1), which is located in Hueston Woods State Park, approximately six miles northwest of Oxford, in Butler and Preble counties, Ohio. Acton Lake is an artificial reservoir, which was created by the construction of an earthen dam across the valley of Four-Mile Creek. The resulting reservoir, which was first flooded in the autumn of 1957, has a maximum

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width of 0.6 km, and a shoreline of 14 km. The maximum depth is about 12 m and the mean depth is 3.9 m. It has a surface of 253 hectares. The lake is a eutrophic body of water and its general physical and chemical characteristics have been described (Winner et al., 1962).

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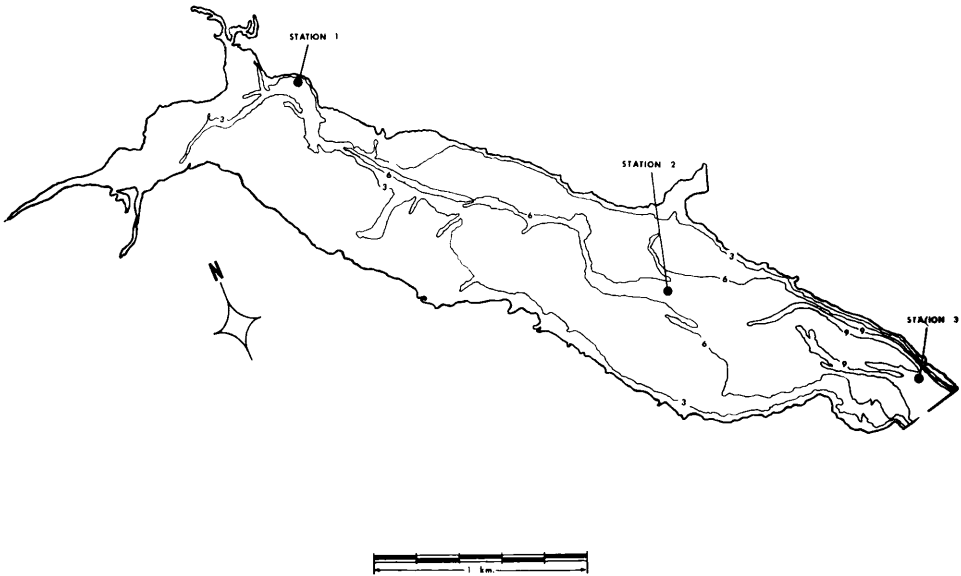


FIGURE 1. Acton Lake, showing collecting stations. Contours in meters.

METHODS

The data discussed in this paper were collected during 1961, 1962, and 1963 from three stations (fig. 1) which were 3, 6, and 9 meters deep. Population data were collected in three ways and these will be referred to as: (1) vertical series data, (2) vertical haul data, and (3) vertical column data.

Vertical series data were collected each of the three years at a single station (station 3, fig. 1). All of these collections were made between the hours of 1100 and 1300 E.S.T. in the following manner. A 3-liter Kemmerer sampler was used to collect plankton from the lake surface and from depths of 3-, 6-, and 9-meters. The 1961 and 1962 collections consisted of seven samplers (21 liters) collected from each depth on each sampling day; the 1963 collections consisted of four samplers (12 liters) collected from each depth on each sampling day. The water from each depth was, separately, strained through a plankton net and bucket of # 20 silk bolting cloth and preserved with formalin. Four discrete samples were collected on each sampling day, one from each depth. The 1961 and 1962 samples were each concentrated to 21 ml; the 1963 samples were each concentrated to 12 ml. This was done in order that each ml of concentrate would be equivalent to an original liter of lake water. Two 1-ml aliquots of the sample from each depth were examined in Sedgwick-Rafter counting cells and a total count was made of each cladoceran species. The average number of individuals in two

cells, then, is taken as an estimate of the number of individuals per liter in the original water sample.

Vertical haul data were collected from all three stations during the 1962 season only. Collecting was begun on April 26 and carried out approximately three times a week at each station until November 17. Each collection was made as follows. A Wisconsin-type plankton net and bucket of # 20 silk bolting cloth was lowered into the water until the rim of the net opening was 3-, 6-, or 9-meters below the lake surface, according to the station being sampled. The net was then hauled vertically to the surface, sampling a column of water the diameter of the net opening (approximately 12 cm). Because of the shallow depth, two such hauls were made and combined into a single sample at station #1. Samples from stations 2 and 3 consisted of a single vertical haul for each sampling day. The station 1 and 2 samples were concentrated to a volume of 11.4 ml and the station 3 samples to a volume of 17.2 ml. Each ml of concentrate was thus equivalent to two liters of lake water filtered during the vertical haul. Two 1-ml aliquots of each sample were examined in Sedgwick-Rafter cells and a total count was made of each cladoceran species. The average number of each species in two cells is utilized as an index of abundance for that species. A comparison of these vertical

TABLE 1
*Daphnia and Bosmina populations according to estimates
from vertical hauls and means of vertical series,
Station 3, 1962*

<i>Daphnia</i>		<i>Bosmina</i>	
Haul	Series	Haul	Series
13	10	1	1
12	12	3	4
19	20	15	28
11	14	17	39
10	3	31	40
1	4	34	39
10	8	27	28
5	4		
2	1		
1	1		

haul indices with population estimates made from vertical series samples, both values representing collections made at the same time from station 3 during the 1962 season, indicate that data yielded by the two methods are quite comparable (table 1). Certainly, these 1962 vertical haul data are adequate for showing seasonal and horizontal distributions of the different species.

Vertical column data were collected from all stations during the 1963 season. This technique was substituted for the vertical haul procedure of 1962. Such collections were initiated on May 6 and all stations were sampled at two- to three-day intervals until November 3. Samples were collected from each station in the following manner. A continuum of 3-liter samples was taken with a Kemmerer sampler from the lake surface to the bottom. Because the sampling cylinder was 50 cm. in length, 6 samples were accumulated in traversing the distance from surface to bottom at station 1; 12 and 18 samples were accumulated from stations 2 and 3 respectively. The entire series of samples from each station was strained through a net of # 20 bolting cloth. Consequently, net plankton were collected from an 18-liter sample at station 1 and from 36- and 54-liter samples at stations 2 and 3. The station 1 and 2 samples were concentrated to 18 ml in formalin, the

station 3 samples to 27 ml. Total cladocerans were counted in two 1-ml aliquots from each station and the average used to estimate the number of each species per liter in the water column.

It is realized that collections made with a Kemmerer sampler may underestimate plankton populations because of the so-called "avoidance reaction" (Pennak, 1957; Ricker, 1938). However, this is also true for other methods of collecting plankton; e.g., the same problem exists in utilizing the Juday plankton trap. Other methods which have been widely used, such as vertical tows and the use of a Clark-Bumpus sampler, may suffer from the same error and also from an additional one, that of loss of organisms due to clogging. In the present study, every effort was made to time events so that the sampler was closed as quickly as possible once the proper depth was attained. Also, population estimates made with a Kemmerer were compared, on a number of days, with collections made by a vertical tow with a plankton net. The two methods agreed well; where there were differences, the population estimates from vertical tow collections were smaller than those from Kemmerer collections, suggesting that avoidance of the Kemmerer sampler by the organisms was not a major problem.

A number of physical factors were also recorded at the times of each sampling of plankton. Factors measured included temperature, pH, dissolved oxygen, free oxygen, alkalinity, incident light, and per cent of clouds in the sky.

SEASONAL DISTRIBUTION OF CLADOCERA

Bosmina longirostris

Plankton sampling was initiated at station 3 on March 28, 1961, and continued on a weekly basis throughout the remainder of the season. *Bosmina*, like other planktonic cladocera of the lake, was not detected in samples collected during the early spring. The first specimen of *Bosmina* was detected in a sample collected on May 23, 1961. In 1962, plankton sampling was begun on April 12, at which time a sampling schedule of collecting from three stations three times each week was established. The first specimen of *Bosmina* was not detected until May 24. In 1963, plankton sampling was initiated on May 6, at which time a sizeable population had already become established. Plankton sampling was terminated on December 4, November 12, and November 3 in 1961, 1962, and 1963, respectively. Small populations of this species were still present on the last day of sampling in all three years. Sometime, between December and March, *Bosmina* disappears, or exists in such low numbers as to be undetected. The species, then, reappears in the plankton samples usually in May. Although Borecky (1956) does not present quantitative data on the seasonal fluctuations of the cladoceran species of Pymatuning Lake, it would appear from her fig. 2 that *Bosmina* was not present in that lake from at least mid-December to mid-January. In contrast, Hall (1964) states that *Bosmina* appears as an important member of the zooplankton of Baseline Lake, Michigan, during the colder months. Although no data are presented, one gets the impression that the species is not present, or is present only in very small numbers, during the warmer months in this Michigan lake.

The seasonal changes in *Bosmina* populations during 1962 and 1963 are illustrated in figure 2. These data are averages for stations 1, 2, and 3 for each day of collection. The spring population was obviously much larger in 1963 than in 1962. This might be, to some degree, due to differences in sampling techniques (vertical haul in 1962 and vertical column in 1963). If anything, the vertical haul method might be expected to underestimate the population at times of maxima, due to potential clogging of the net and consequent failure of the water to pass freely through. On the other hand, comparable data are available from vertical series collections made at station 3 for the years 1961, 1962, and 1963. These are averages of samples collected from the surface and from depths of 3-,

6-, and 9-meters at one-week intervals. These data substantiate that spring populations were much larger in 1963 than in either 1961 or 1962.

The peak population was not only larger in 1963 than in 1962, but also developed much earlier (fig. 2). The maximum population was recorded in May, 1963; in 1962, the population did not grow appreciably until mid-June and the maximum 1962 population did not occur until July. Evidently, conditions were more favorable for this species and some condition promoted earlier development of the population in 1963. Weekly water temperature records are available from four depths for both 1962 and 1963 (fig. 3). Surface and 3-meter-depth temperatures were considerably higher in May of 1962 than in May of 1963. In 1963, the surface temperature did not exceed 27°C until late June, whereas in 1962, a surface temperature of 29°C was recorded on May 17. In contrast, water at the 6-meter depth warmed up earlier in 1963; thus, the temperature of the deeper strata seem to have had more influence on the rate of development of the population than did the temperature of the shallower water.

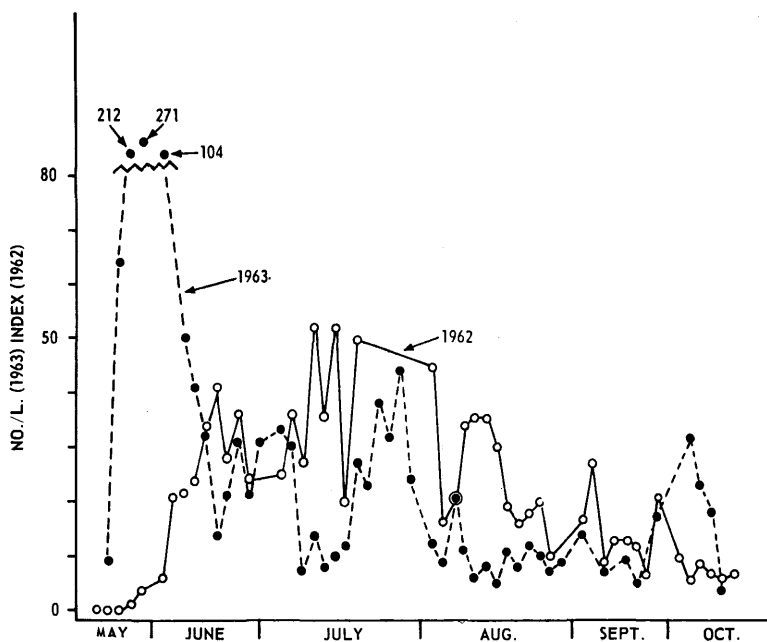


FIGURE 2. *Bosmina* populations. Each point is an average, calculated from samples of the entire water column at stations 1, 2, and 3.

This apparent correlation between the rate of development of the spring population and the rate of warming of the deeper water strata would be logical if the entire late winter and early spring populations were concentrated in the deeper water. Although there is insufficient knowledge of the species life cycle to substantiate such a situation, there are at least three hypotheses which would account for it: (1) the eggs of this species cannot tolerate desiccation and/or freezing. The water level of Acton Lake is lowered approximately 3 meters each November. An extensive area of bottom sediment is thus exposed and remains so until the lake refills, usually in mid- or late March. This would eliminate the shallow water population each winter. (2) The species does not produce ephippial eggs until after the water level is lowered each year. Again, this would eliminate the shallow water population each winter. (3) The species does not produce

ephippial eggs and the spring population arises from a few overwintering adults which have concentrated in deep water. These three hypotheses are currently being tested.

The data of figure 3 also suggest an explanation for the populations of 1963 being much larger than those of 1962. Vertical mixing of the water column, obviously, was effective to greater depths in 1963 as evidenced by the much higher temperatures of the 6-meter stratum during that year. It is generally assumed, other factors being equal, that productivity is proportional to the depth of mixing in a body of water (Rawson, 1960). If this is true, then the 1963 season should have provided a greater food supply for planktonic cladocera and this could have been a major factor contributing to the larger populations. With the exception of *Diaphanosoma leuchtenbergianum*, the populations of all Cladocera were larger in 1963 than in 1962 (fig. 4, 5, 6).

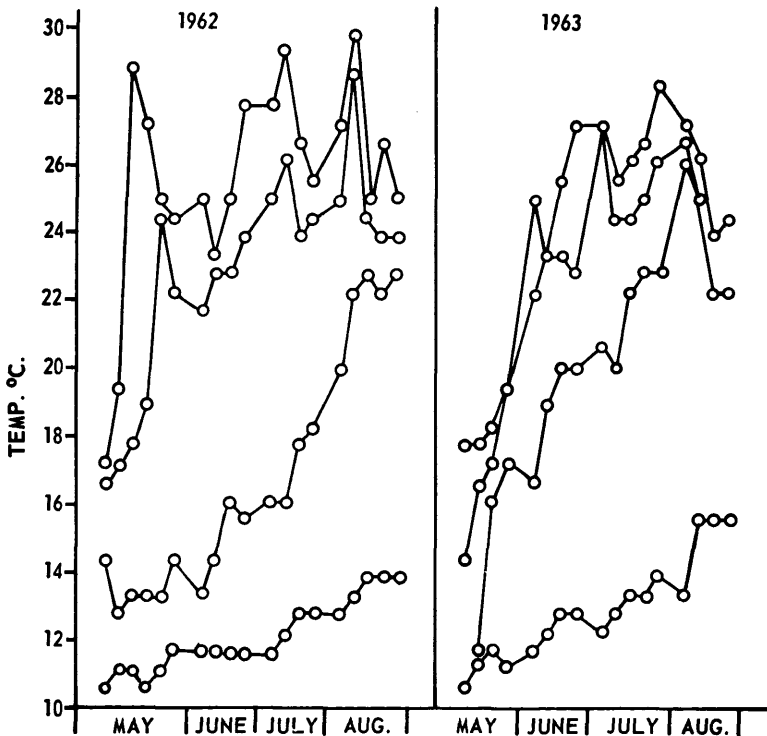


FIGURE 3. Surface, 3-, 6-, and 9-meter water temperatures, station 3.

Daphnia parvula

This species first appeared in the 1961 collections of March 26 as 0.5 individual per liter, but was not detected again until April 27, again as 0.5 individual per liter. It did not reappear in collections until May 25, and was thereafter consistently present in samples throughout the remainder of the spring and summer. In 1962, the species was first detected on May 11 and, in 1963, there was already a population established when collecting was begun on May 6. The species was still present on the date of the last collection in all three years. Like *Bosmina*, *Daphnia* seems to disappear from the plankton during the winter, to reappear in April or May.

The seasonal changes in *Daphnia* populations during 1962 and 1963 are depicted in figure 4. It is obvious that *D. parvula* is a vernal species, attaining its maximum populations in May, declining in numbers through June, and persisting in only small numbers throughout the summer and into the autumn. The 1961 data from station 3 indicate a minor autumnal peak that was lacking in 1962.

Like *Bosmina*, *Daphnia* populations were much larger in 1963 than in 1962. Again, this may be a reflection of the deeper mixing of the water column in 1963. Unlike *Bosmina*, there was no appreciable difference in the time of development of the spring population of *Daphnia* between the two years. Because the early warming of the 6-meter stratum in 1963 and the early warming of the surface and 3-meter water in 1962 (fig. 3) had no differential effect on the rate of development of the spring populations, one would suspect that the rate of population growth ceases to respond to temperature at relatively low temperatures. Because the

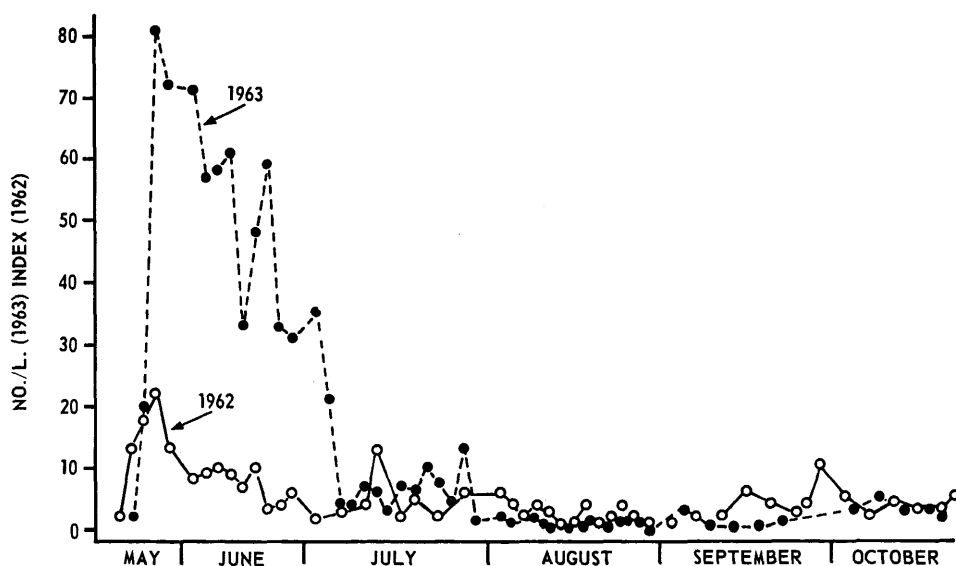
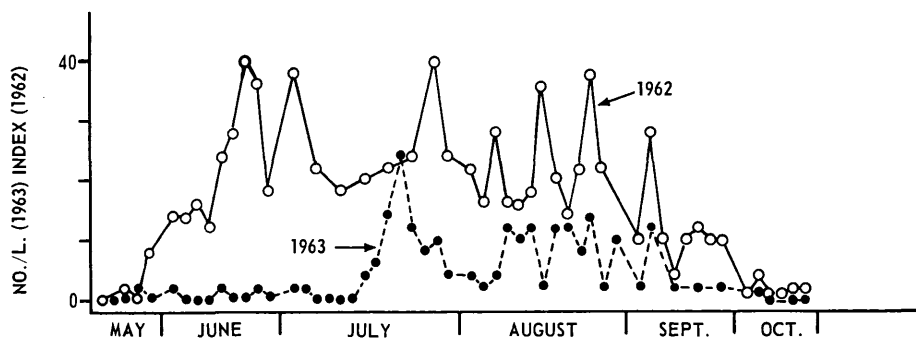


FIGURE 4. *Daphnia* populations. Legend as for figure 2.

1963 population was so large and because the surface, 3-, and 6-meter water temperatures were, for the most part, below 25°C, it seems likely that optimum temperatures for the species are below that temperature. This concept also fits the vertical distribution of the species, since its population maxima most frequently occurred at a depth of 6 meters. The temperature, at this depth, rarely exceeds 23 or 24°C throughout the summer and early fall period.

Diaphanosoma leuchtenbergianum

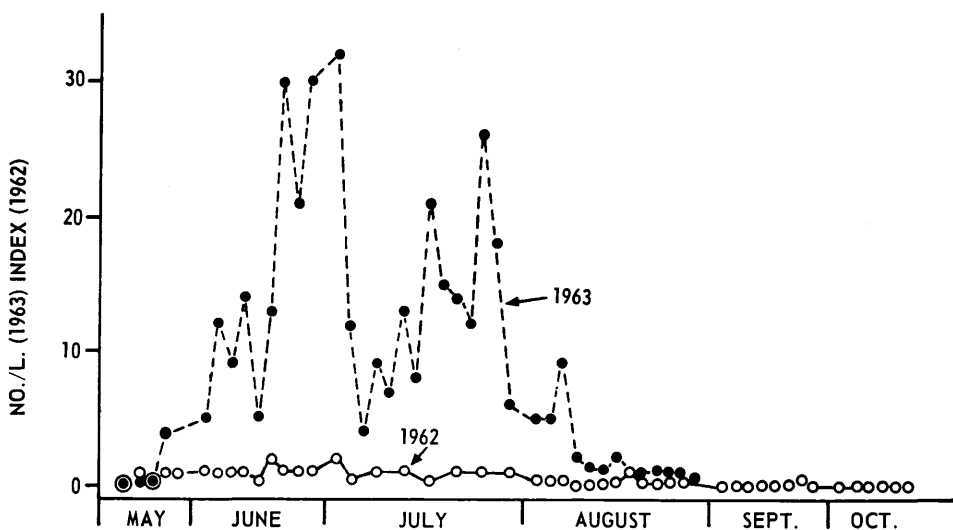
This cladoceran was first detected in plankton samples on June 13 in 1961, on May 24 in 1962, and on May 24 in 1963. Although collections were made until December 4, the species was not detected in samples collected on, or after, October 9 in 1961, but was still present as fractions of an individual per liter on the last days of sampling in 1962 and 1963 (Nov. 12 and 3, respectively). Seasonal changes in the populations of *Diaphanosoma* are depicted in figure 5. It is obvious that the buildup of its population lags considerably behind that of the other Cladocera in the spring and that it declines in numbers earlier in the autumn. This is probably a consequence of its being a polythermic species, as suggested by

FIGURE 5. *Diaphanosoma* populations. Legend as for figure 2.

Ruttner (1963). This suggestion is substantiated in two ways by the data of the present study. First, *Diaphanosoma* differs from all the other Cladocera in that its population peak came much earlier in 1962 than in 1963. There was a sizable population in early June, 1962, but such a population size was not reached in 1963 until mid-July. This was associated with an early warming of surface and 3-meter water in 1962 (fig. 3). Second, this is the only cladoceran species whose populations were larger in 1962 than in 1963. Again, the most probable cause is that the shallow water was warmer for most of the spring and summer of 1962 than it was in 1963, and data on horizontal distribution indicate that this is a shallow water species in Acton Lake. Borecky (1956) also records this as a summer form, being important in the plankton of Pymatuning Lake only during July and August.

Ceriodaphnia quadrangula

The only continuous data for 1961 are the vertical series samples from station 3. *Ceriodaphnia* occurred as a very minor component of the plankton samples from this station and, then, only from mid-September into October. Although complete vertical series samples were not taken prior to June 16, 1961, surface and

FIGURE 6. *Ceriodaphnia* populations. Legend as for figure 2.

9-meter samples were collected at station 3 and a mid-water sample was taken at station 1 on a weekly basis starting on March 28. The species was never found in these spring and early summer samples. Figure 6 depicts the 1962 and 1963 populations of this species. In 1962, the index of abundance for this species never exceeded a value of two and an autumn population did not develop at station 3 as it did in 1961. In 1963, this species unaccountably increased in numbers to such a degree that it comprised a substantial portion of the cladoceran community during June, July, and August. It declined drastically in numbers during the latter part of August and was virtually absent from the plankton during September, October, and November. In summary, it occurred as a minor component of the 1961 plankton during the autumn only, was virtually absent during the 1962 season, and was an important component of the plankton from late spring into the summer of 1963. In several other southwestern Ohio reservoirs, where this species is the numerically dominant planktonic entomostracan, it is abundant from May into October (Winner, unpublished data). This is a striking example of the dangers inherent to drawing conclusions about planktonic communities from a single year's data, or of concluding that a species will necessarily behave the same in different bodies of water.

HORIZONTAL DISTRIBUTION AND RELATIVE ABUNDANCE

Collections from 3 stations give some insight into the horizontal distribution and relative abundance of the four cladoceran species. Relative abundance has been computed for each species by determining its percentage of the total cladocerans counted in 2 Sedgwick-Rafter cells from each station for each day of the vertical haul and vertical column samples of 1962 and 1963, respectively. These percentages can be considered as indices of relative abundance of each species for different seasons, years, and locations in the lake. The 1962 data are presented in figure 7 as monthly averages.

Bosmina longirostris

This was the numerically dominant planktonic cladoceran at all three stations during both years. Considering the 300 available samples (50 from each station during each year), *Bosmina* was the most abundant cladoceran in 53 per cent of the samples from station 1, 75 per cent of the samples from station 2, and 85 per cent of the samples from station 3. Its relative importance, thus, increased slightly toward the deeper end of the lake.

Daphnia parvula

Daphnia exhibited no apparent "preference" for any of the three stations (fig. 7). During both years, there was a period during the spring when *Daphnia* was the numerically dominant species at all three stations. This occurred in May of 1962 and preceded the development of the *Bosmina* population. In 1963, however, *Daphnia* did not assume dominance until June, at which time it did so in spite of an already well-established *Bosmina* population.

This would suggest that the summer low in *Daphnia* populations is not primarily due to competition with *Bosmina*, but to the development of environmental conditions (e.g., higher temperatures, light intensities, inadequate food, etc.) that are unfavorable to the former species. It should also be mentioned that there is increasing evidence that predation may substantially reduce the populations of some Cladocera. Hall (1964) has suggested that the midsummer low in populations of *Daphnia galeata mendotae* is partially a consequence of predation by *Leptodora* and is not entirely due to inadequate food supply, as has usually been supposed. Brooks and Dodson (1965) have presented strong circumstantial evidence that larger zooplankters are virtually eliminated from Connecticut lakes by alewife predation. Straškraba (1965) has noted that fish predation can mark-

edly affect the composition of planktonic communities and, especially, that predation is associated with the replacement of *Daphnia* by *Bosmina*. Acton Lake does support large populations of the gizzard shad, *Dorosoma cepedianum*, which is a very efficient planktivore (Kutkuhn, 1957; Price, 1963). *Daphnia parvula*, being a larger animal than *Bosmina longirostris*, would probably be more vulnerable to shad predation. In southwestern Ohio, reservoirs having shad populations support small summer zooplankton populations dominated by *Bosmina longirostris*, whereas reservoirs lacking this fish species have much larger summer zooplankton

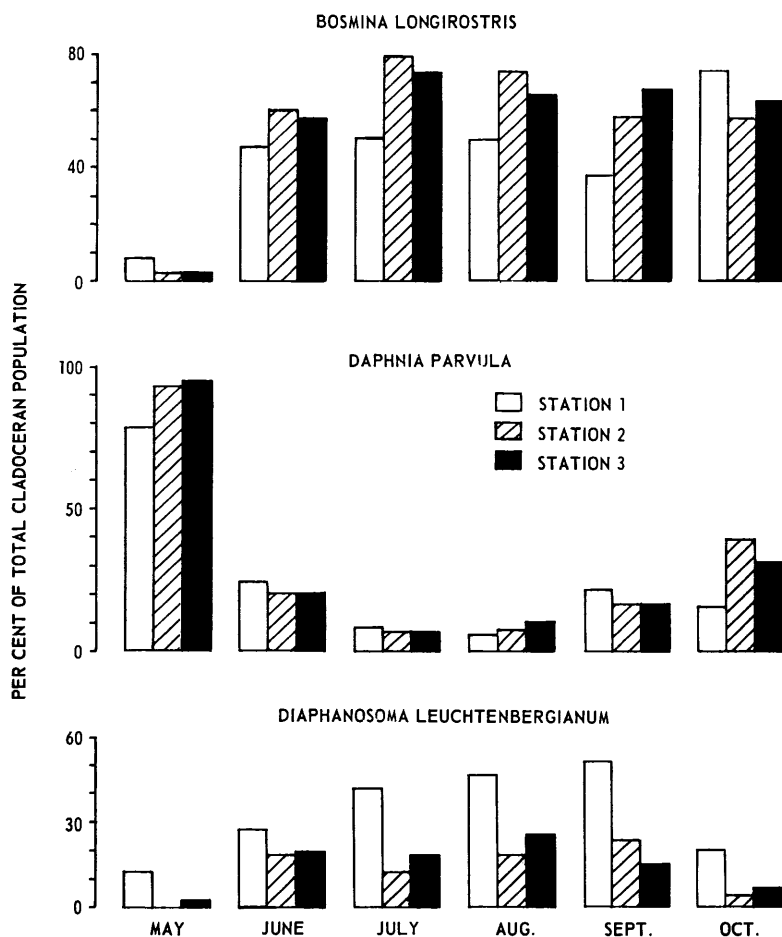


FIGURE 7. Relative monthly abundance of 3 cladoceran species at each of 3 stations, 1962. Relative monthly abundance is expressed as the percentage each species comprised of the total number of individuals of all species in samples of the entire water column.

populations dominated by *Ceriodaphnia quadrangula* and *Daphnia* spp. (Winner, unpublished data). The decrease in numbers of *Daphnia* during the summer in Acton Lake could, thus, be a consequence of predation by shad. Although the actual populations were quite small, the October populations of *Daphnia* were second in size only to those of *Bosmina*.

Diaphanosoma leuchtenbergianum

This was the only one of the four species to be consistently most abundant at a single station (fig. 7). *Diaphanosoma leuchtenbergianum* obviously favors the shallow-water station (station 1), where it was frequently the most numerous cladoceran and always comprised a significant proportion of the community during its somewhat limited seasonal occurrence. It was the most abundant species at station 1 on 25 of the 100 sampling days; it was never the most numerous species at either stations 2 or 3, and was usually present at these stations only in small numbers, even when it was present in large numbers at station 1. This was especially true during the 1963 season.

Ceriodaphnia quadrangula

This species was of numerical importance only during the 1963 season from June through August. It was actually the dominant cladoceran in 20 per cent of the samples collected during its period of occurrence, three samples from station 1, six from station 2, and one from station 3. It attained about the same relative abundance at all three stations, exhibiting no apparent preference for any of the three.

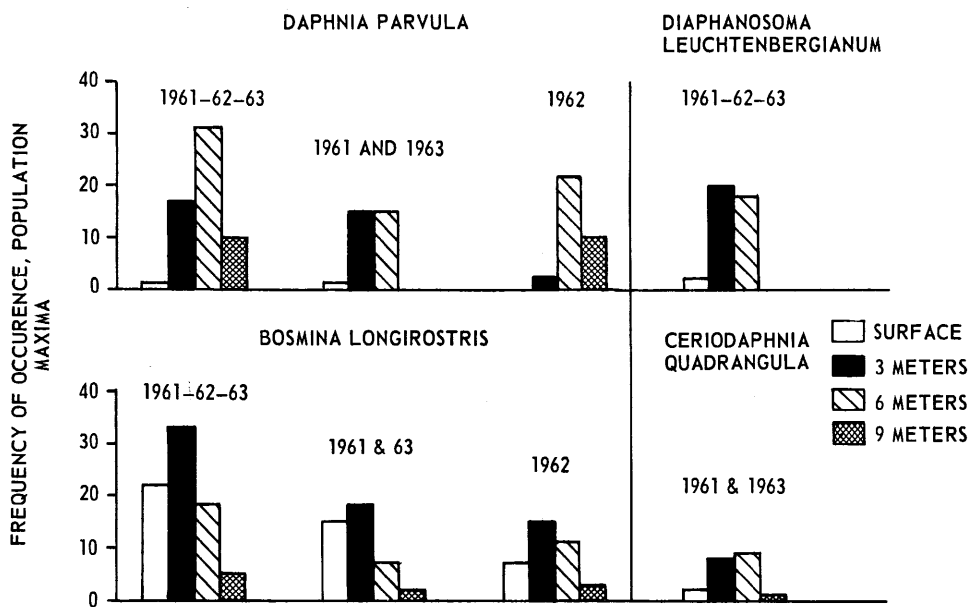


FIGURE 8. Frequency at which maximum numbers of each of 4 cladoceran species occurred in samples from the surface and from depths of 3, 6, and 9 meters, station 3.

VERTICAL DISTRIBUTION

As would be expected, vertical distributions varied from day to day, from species to species, from season to season and, in some cases, from year to year. One method of summarizing such variation is to tabulate the sample depth or depths at which the greatest number of individuals of each species occurred for each sampling day. Figure 8 presents such a tabulation for each species. All samples were collected from station 3 between the hours of 1100 and 1300 (vertical series data).

On many days a species was more abundant at one sampling depth than at any of the others (i.e., the estimate of population size was at least 20 per cent greater

than the estimate for any other depth). Such a day contributed only one frequency-of-occurrence datum to figure 8. Sometimes, however, a species was about equally abundant at two depths during a single sampling period (i.e., less than 20 per cent difference between the population estimates for the two depths); rarely, a species was about equally abundant at three depths in a vertical series. Such days each contributed two or three frequency-of-occurrence data to figure 8. For example, in 1962, maximum numbers of *D. parvula* never occurred at the surface, occurred at 3 meters three times, at 6 meters twenty-one times, and at 9 meters ten times.

Bosmina longirostris

This discussion is based on fifty-three vertical series collections, 13 from 1961, 24 from 1962, and 16 from 1963. The data of figure 8 agree with data on seasonal and horizontal distribution in indicating *Bosmina* as the most cosmopolitan planktonic cladoceran in Acton Lake. Although samples from the 3-meter depth most commonly contained the largest numbers of this species, it frequently at-

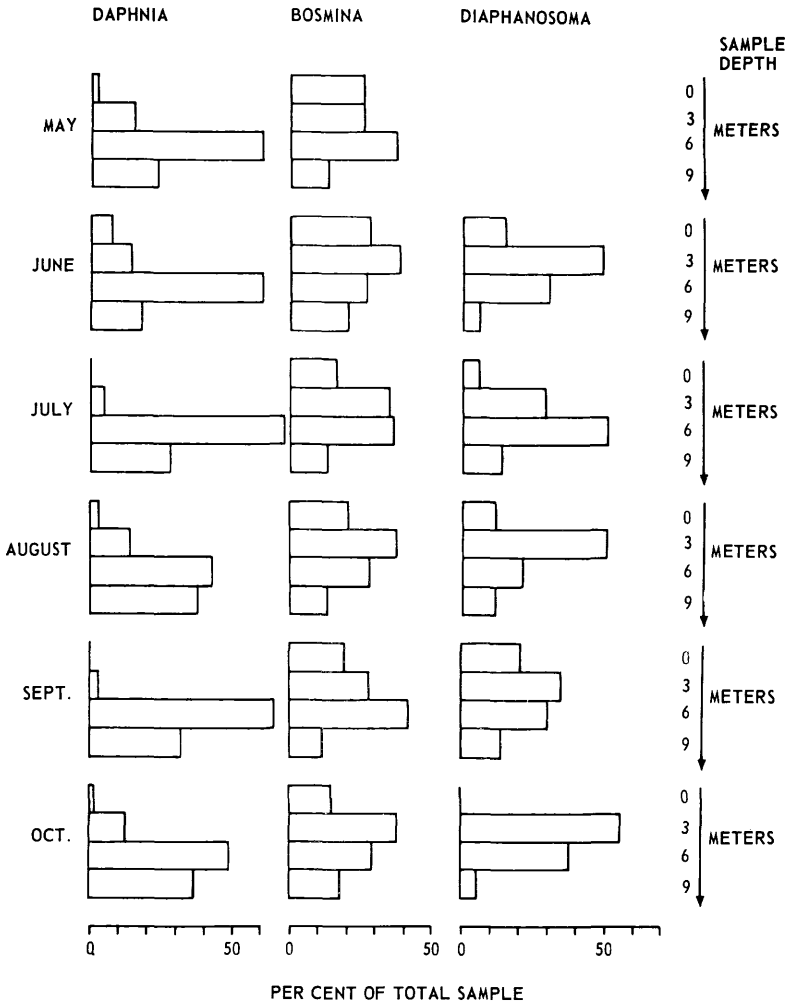


FIGURE 9. Mean monthly vertical distribution of 3 cladoceran species at station 3 during 1962.

tained its maximum abundance at 6 meters, and it was the only cladoceran that also reached its greatest abundance in surface-water samples in a number of cases. The relatively few occurrences of population maxima at the 9-meter depth are probably a reflection of the fact that, during part of June, and all of July, August, and September, there is little or no free O_2 at this depth in Acton Lake (Winner et al., 1962).

A comparison of the 1962 vertical series data with such data from 1961 and 1963 indicates that the species was localized more deeply in 1962 than in the other two years (fig. 8). This was even more true in the case of *Daphnia*; possible reasons for this will be presented later in a section discussing the vertical distribution of the latter species. Figure 9 depicts the vertical distribution of *Bosmina* on a monthly basis for the 1962 season. The values plotted represent the per cent of the population at each depth as monthly averages. Space will not permit presenting the vertical distribution of *Bosmina* on each of the 53 days for which such data are available. The vertical distribution was, however, extremely variable from day to day in regard to the depth at which the maximum population occurred.

Concurrent with the collection of the plankton samples, the following factors were measured at each depth: temperature, pH, dissolved oxygen, free carbon dioxide, phenolphthalein and methyl orange alkalinity, and, beginning on July 20, 1962, per cent of incident light. Secchi disc transparency was also measured at each sampling period, as was per cent of sky covered by clouds. Attempts to relate the vertical distribution of *Bosmina* to these instantaneous measurements of environmental factors were not rewarding. This is not surprising for, according to Ringelberg (1964), the phototactic swimming response of *Daphnia magna* is a correction for the change in prevailing light intensity and the actual stimulus is a function of the rate of change. Thus, to correlate the vertical position of a species with current light conditions, one must take into account: (1) the rate of light intensity change, because this provides an index of stimulus; (2) the absolute light intensity to which the plankters have become adapted, because this may influence the threshold value of the stimulus; and (3) the turbidity of the water, because the swimming response to a given light intensity change should occur in a shorter distance in turbid than in clear water. Also, as Bainbridge (1961) has pointed out, the response of plankters to environmental conditions, in general, is somewhat dependent on conditioning to prior environmental circumstances. It would seem, then, that any attempt to detect correlations between the vertical distribution of a species and environmental factors would be profitable only if the past history of the population relative to those environmental factors were known.

The variability in the day-to-day vertical distribution of *Bosmina* may also reflect its small size (the smallest of the 4 species) and, possibly, its weak swimming ability. More so than the other three species, it is conceivably more frequently at the mercy of vertical turbulence.

Frequently, individuals of this species were present in samples collected from the 6- or 9-meter depths in which oxygen was not detectable by the Alsterberg modification of the Winkler method (A.P.H.A., 1960). These individuals were intact, apparently functional organisms. They could be seen swimming in the collecting vial prior to the addition of formalin. They were examined under a dissecting microscope on one occasion and appeared to be in good condition. The collections, of course, do not indicate how long *Bosmina* could or did survive in this oxygen-free zone; they may actually have little tolerance to sustained periods of oxygen depletion. It may be that they simply make periodic forays into this zone from overlying oxygenated strata. It may also be that they wander into this stratum and eventually perish, being unable to extricate themselves due to a reduction in metabolic rate mediated by insufficient oxygen. It is also possible that they are senescent individuals, unable to maintain their position in the water column.

Daphnia parvula

This discussion is based on 54 sampling days, 13 in 1961, 27 in 1962, and 14 in 1963. *Daphnia* was most abundant in samples collected from the 6-meter depth, maximum numbers being found at this depth on 56 per cent of all sampling days during 1961, 1962, and 1963. The tendency of this species to localize at 6-meters was most pronounced in 1962, when maximum numbers occurred in samples from this depth on 64 per cent of the sampling days; in contrast, only 48 per cent of the combined 1961-1963 maxima occurred in samples from this depth (fig. 8). It is also noteworthy that only 6 per cent of the 1962 maxima were from the 3-meter depth, whereas 56 per cent of the 1961-1963 maxima were in samples from that depth. Finally, 30 per cent of the 1962 maxima were collected from 9 meters, but none of the 1961-1963 maxima came from that depth. Thus, it appears that *Daphnia* localized more frequently at 6 meters in 1962 and was, in general, distributed more deeply in that year than in the other two years.

Because the maximum rate of population growth and the maximum population size of this species occurred in May, one would suspect that optimum environmental conditions would include relatively low temperatures and light intensities well below those of subsequent months. This is generally assumed to be true of vernal species. The localization of *Daphnia parvula* in deeper water strata during the summer of 1962 fits this hypothesis nicely. It would follow, then, that the more frequent localization of the species at the 3-meter depth during 1961 and 1963 might reflect lower temperatures and/or lower light intensities at that depth during these years. The data, however, do not support this speculation. The 3-meter stratum was not significantly cooler (fig. 3) and Secchi disc transparencies were not appreciably less in 1961 and 1963 than in 1962. Also, fluctuations in water temperature and transparency from sampling period to sampling period do not correspond to changes in the vertical distribution of the species. None of the other factors measured (free CO₂, pH, dissolved O₂, and alkalinity) show any relationship to the vertical distribution of *Daphnia*.

Dissolved-oxygen concentrations during the 3-year interval deserve some further comment. The 6-meter oxygen concentrations were, in general, lower in 1962 than in 1961 or 1963. The 1962 populations concentrated in 6- and 9-meter strata in spite of low oxygen concentrations, whereas the 1961 and 1963 populations were frequently concentrated in warmer, upper strata in spite of adequate, available oxygen in cooler, deeper strata.

These differences in the depth distribution of *Daphnia* during the three years must either be independent of changes in environmental factors, must be related to these factors in some undetected way, or perhaps, are related to some environmental factor or factors that have not been measured. The first possibility seems highly unlikely and nothing meaningful can be said about the second. However, the temperature data presented in figure 3 strongly suggest that an unmeasured factor is responsible for the discrepancy in vertical distribution patterns from year to year. Note that in 1962 there was a considerable difference between the 3- and 6-meter water temperatures. In 1961 and in 1963, the temperature differences between these two strata were considerably less. It has already been pointed out that the 6-meter oxygen concentrations were lower in 1962 than in 1961 and 1963. Thus the 6-meter stratum was effectively below the epilimnion during 1962, but was within or at the lower boundary of the epilimnion during 1961 and 1963. This means that there was more vertical mixing of the water between the 6-meter stratum and the surface in 1961 and 1963 and, considering the steady and rapid increase in 6-meter water temperatures in 1961 and 1963, it would seem logical that *Daphnia* were more frequently mixed throughout the epilimnion during those years. The days on which maximum *Daphnia* populations occurred at the surface and at the 3-meter depth may have been days of considerable vertical turbulence. It is suggested, then, that the vertical distribution during 1962 was determined by the species and took advantage of the cooler temperatures

and lower light intensities of the lower strata, whereas, in 1961 and 1963, the vertical distribution was markedly influenced by a factor extrinsic to the species, vertical turbulence of the water column.

Diaphanosoma leuchtenbergianum

Most of the vertical distribution data for this species were collected during the 1962 season, because the species was present only occasionally and in small numbers at station 3 during the 1961 and 1963 seasons. The following discussion is based on 40 vertical series collections, 8 from 1961, 27 from 1962, and 5 from 1963. These data are summarized in figure 8 and on a monthly basis for 1962 in figure 9. This species was obviously a mid-water inhabitant at station 3 during the period of collection, population maxima being recorded with almost equal frequency at the 3- and 6-meter depths, rarely at the surface, and never at the 9-meter depth (fig. 8). This vertical distribution pattern is somewhat surprising in view of the fact that the species shows a marked preference for station 1 over stations 2 and 3 and one might thus expect it to concentrate toward the surface when occupying the deeper portion of the lake. The fact that it does not raises the question as to whether it prefers shallow water or whether it is, in reality, a form that lives in proximity to the bottom. If the latter were true, it would tend to accumulate at intermediate depths at station 3, deeper water being unfavorable because of a lack of oxygen and low temperatures.

Ceriodaphnia quadrangula

The discussion of the vertical distribution of this species is based on only 16 vertical series collections, 4 from 1961 and 12 from 1963. The 1961 populations were present only in September and October, whereas the 1963 populations were present from late May until mid-August. The limited data suggest that this is a mid-water form, maximum populations usually occurring at 3- and/or 6-meter depths (fig. 8).

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